

Acclimation of *Saccharomyces cerevisiae* to Low Temperature: A Chemostat-based Transcriptome Analysis

Tai, S. L., Daran-Lapujade, P., Walsh, M. C., Pronk, J. T., & Daran, J. M. (2007) *Molecular Biology of the Cell*, 18, 5100-5112.

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Outline

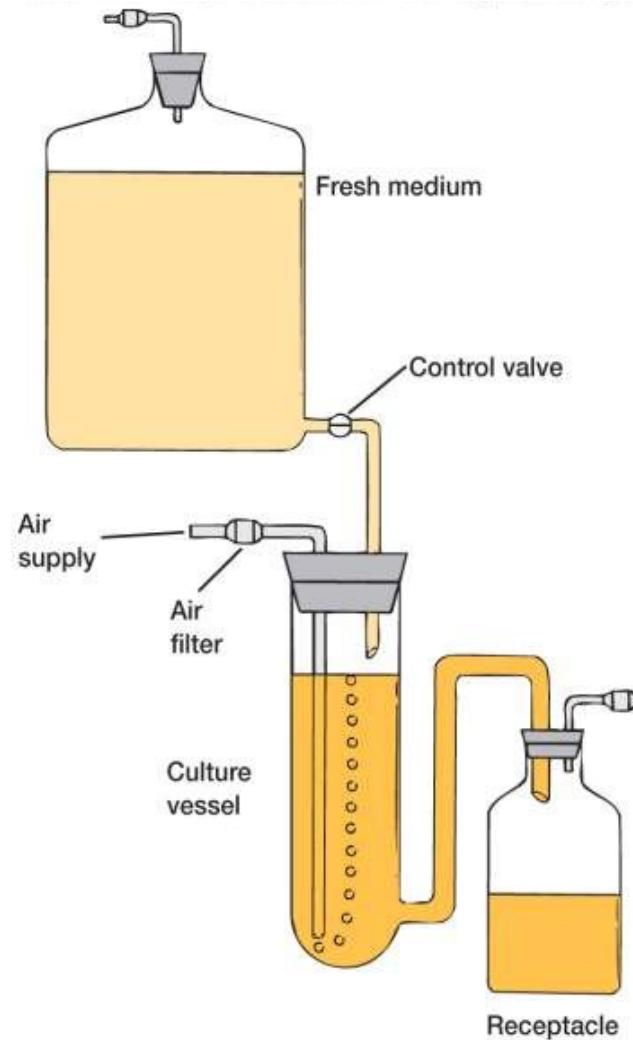
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Chemostat Culture Allows For Fixed Experimental Conditions

- **Chemostat culture** involves the continuous addition of fresh medium.
- Allows for control of growth factors.
- Specific growth rate can be measured accurately.
- Batch culture is a closed system which does not allow for accurate measurement of specific growth rate.



Low-temperature Acclimation and Cold Shock Have Differing Results

- Cold shock entails a rapid decrease to near freezing temperatures.
- Low-temperature acclimation is the biological response of cells to steady decreases to near freezing temperatures.
- Trehalose is required for transcription in low temperature situations.
 - Not present in low temperature acclimation results.

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S. Cerevisiae Grown In Varying Conditions of Temperature and Nutrient Content

Limiting nutrient	Growth temperature (°C)	$Y_{\text{Glu}/X}$ (g _{DW} · g _{glucose} ⁻¹)	q _{Glu} ^a	q _{EtOH} ^a	q _{CO2} ^a	Carbon recovery (%)	Residual glucose (mM)	Residual ammonia (mM)
Glucose	12	0.07 ± 0.01	-2.5 ± 0.2	3.8 ± 0.3	4.4 ± 0.3	100 ± 3	2.8 ± 1.1	65.2 ± 2.2
Glucose	30	0.07 ± 0.00	-2.3 ± 0.0	3.5 ± 0.0	3.8 ± 0.2	95 ± 1	0.3 ± 0.1	61.3 ± 4.5
Ammonium	12	0.05 ± 0.00	-3.6 ± 0.2	6.1 ± 0.3	6.0 ± 0.6	97 ± 4	90.0 ± 9.8	1.5 ± 0.2
Ammonium	30	0.04 ± 0.00	-4.0 ± 0.1	6.8 ± 0.2	7.4 ± 0.2	97 ± 2	85.1 ± 8.2	0.2 ± 0.1

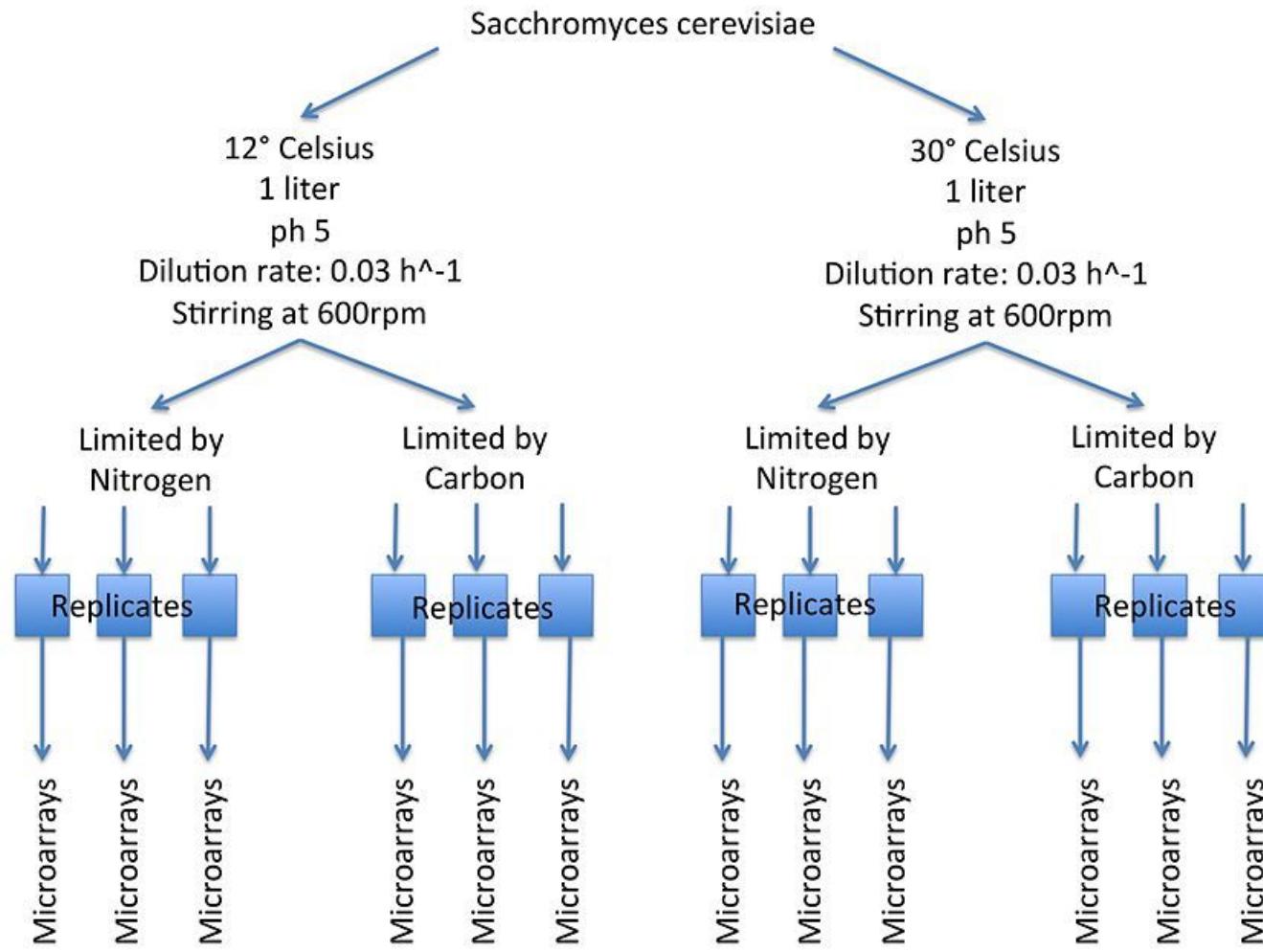
Cultures were grown at 30 and 12°C (D = 0.03 h⁻¹). Values represent the mean ± SD of data from three independent steady-state chemostat cultivations. $Y_{\text{Glu}/X}$, biomass yield on glucose; DW, dry weight.

^a Values expressed as mmol · g_{DW}⁻¹ · h⁻¹.

Table 1

- *S. Cerevisiae* is minimally affected by variation in temperature.
- Higher temperatures correlated with lesser amounts of a limiting nutrient corresponding residual residue.
 - Larger amounts of residual glucose at 12°C connected to possible contamination of gene sets.

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Temperature and Nutrient Limitations Were Analyzed Using DNA Microarray Analysis

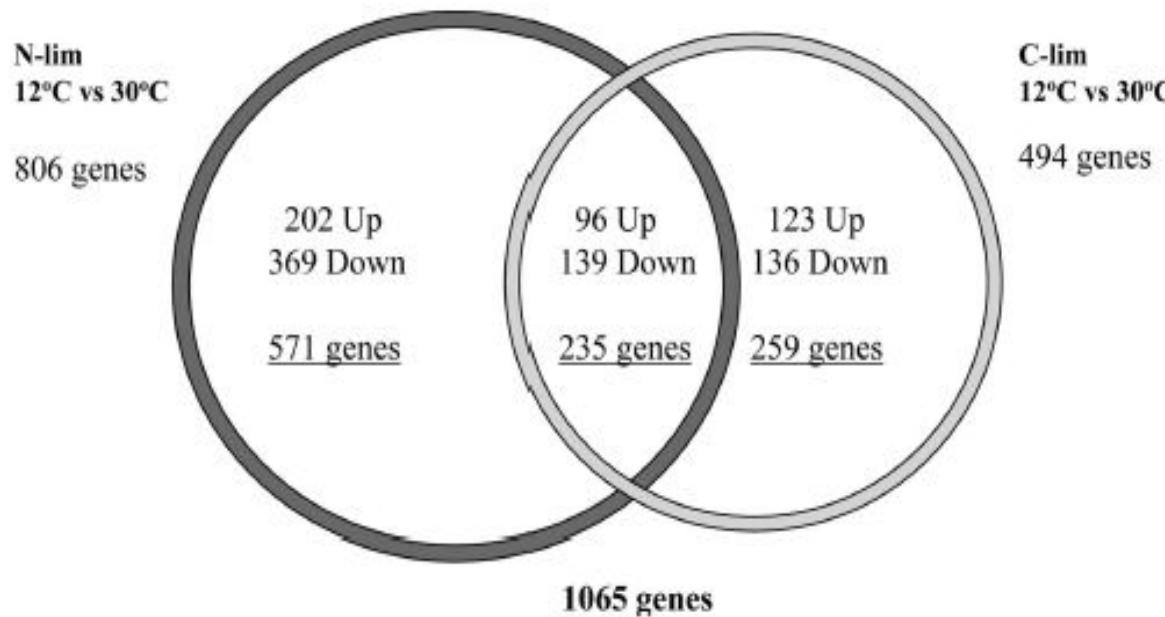
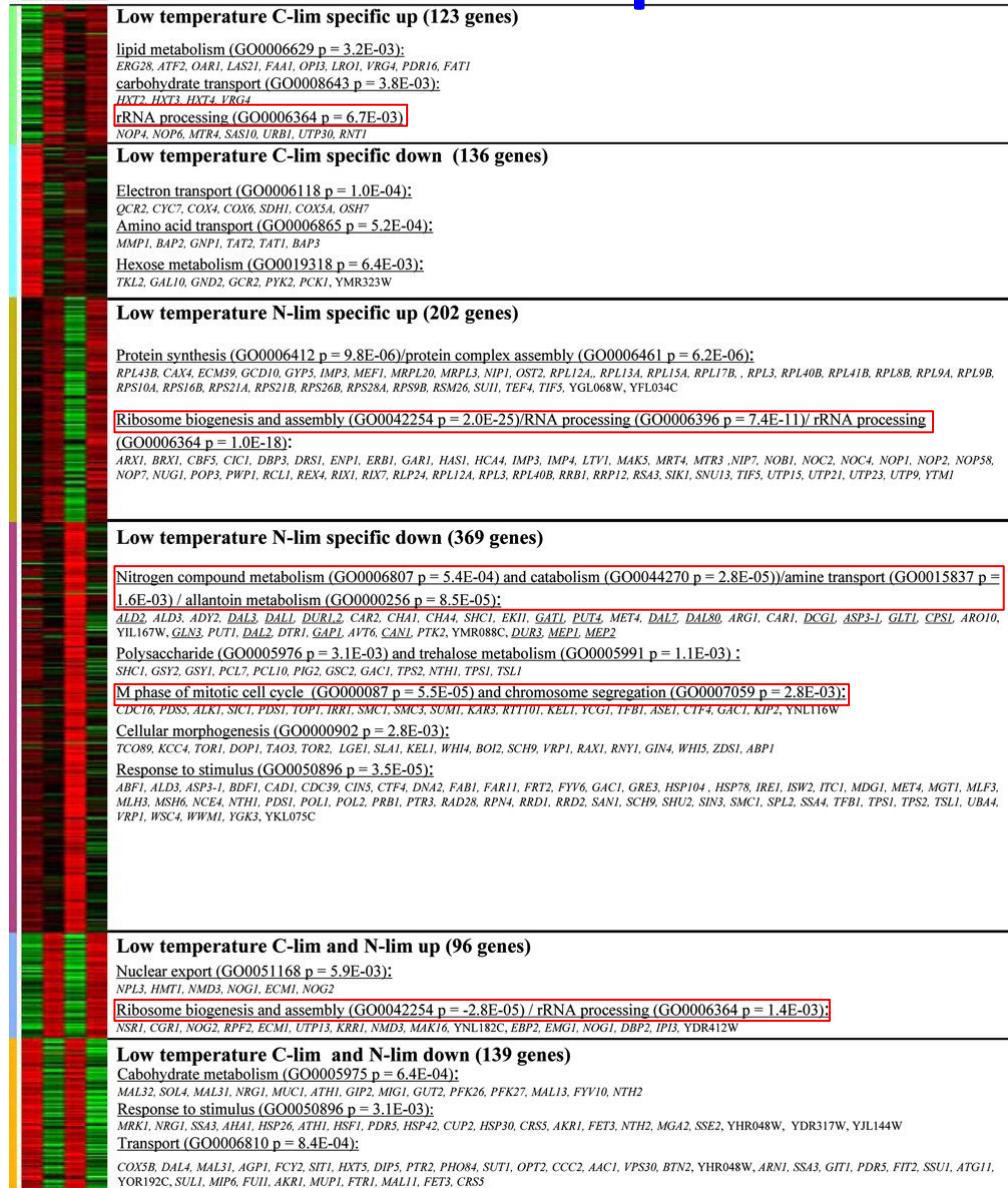


Figure 1

- 1065 represents the number of temperature responsive genes in *S. cerevisiae* genome.

Heat Mapping Was Used To Identify Transcription Level of Temperature Responsive Genes



- Goal was to identify regulatory networks involved in acclimation of *S. cerevisiae* to low temperature.
- Observed changes in
 - Transporters of limiting nutrient
 - Translational machinery
- NCR genes and catabolite repression underlined

Figure 2

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S. cerevisiae Stores Protein and Carbohydrate In Chemostat Culture

Limiting nutrient	Growth temperature (°C)	Biomass dry weight (g _{DW} · l ⁻¹)	Whole cell protein (g _{protein} · g _{DW} ⁻¹)	Biomass nitrogen content (mg _{nitrogen} · g _{DW} ⁻¹)	Trehalose (g _{equivalent glucose} · g _{DW} ⁻¹)	Glycogen (g _{equivalent glucose} · g _{DW} ⁻¹)
Glucose	12	1.71 ± 0.09	0.40 ± 0.01	nd	<0.005	0.06 ± 0.01
Glucose	30	1.89 ± 0.06	0.43 ± 0.01	nd	0.02 ± 0.00	0.04 ± 0.00
Ammonium	12	2.27 ± 0.05	0.47 ± 0.03	63 ± 3	<0.005	0.02 ± 0.00
Ammonium	30	3.53 ± 0.01	0.34 ± 0.01	41 ± 2	0.04 ± 0.00	0.05 ± 0.01

Cultures were grown at 30 and 12°C (D = 0.03 h⁻¹). Values represent the mean ± SD of data from three independent steady-state chemostat cultivations. DW, dry weight; nd, not determined.

Table 2

- Trehalose and glycogen biosynthesis occurs under stress conditions.
 - Biosynthesis varies with temperature.
- Reason for storage of carbohydrates in nonfreezing temperature is unclear.
 - Trehalose was not produced in *tps1* and *tps2* strains, yet did not affect viability.

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Promoter Analysis Reveals Regulation Trends in Gene Regulation

(A) 5' upstream cis-regulatory motif

Regulatory cluster	Motif name	Putative-binding protein	Promoter element	occ ^a	Expected occ ^b	occ E ^c
Low Temperature C-lim Up	—	—	TGAAAAAA	206	113.04	2.30E-11
Low Temperature C-lim Up	—	—	CGATGAG	57	17.49	6.1E-14
Low Temperature N-lim Up	PAC	—	TGAGATG	49	16.3	4.1E-07
Low Temperature N-lim Down	GATAA	Gln3/Gat1/Dal80/Gzf3	AGATAAG	203	102.57	3.1E-15
Low Temperature C- and N-lim Up	STRE	Msn2/Msn4	ACCCCTT	29	8.73	1.6E-03
Low Temperature C- and N-lim Up	PAC	—	CGATGAG	30	8.39	5.0E-05
Low Temperature C- and N-lim Down	—	—	CGTCCAC	13	2.85	7.8E-03

(B) Overrepresentation of transcription factors (TF) binding targets

Regulatory cluster	Factor	p value	K ^d	P ^e
Low Temperature C-lim Up	Mbp1p	1.6E-03	10	65
Low Temperature C-lim Down	Hap2-Hap1	3.9E-05	3	4
Low Temperature N-lim Up	Hap3-Hap1	9.9E-06	3	3
Low Temperature N-lim Up	Fhl1p	3.4E-05	19	203
Low Temperature N-lim Up	Sfp1p	1.3E-03	7	51
Low Temperature N-lim Down	Gln3p	2.1E-07	20	92
Low Temperature N-lim Down	Gln3-Dal82	5.5E-07	8	15
Low Temperature N-lim Down	Hap2-Dal82	6.8E-05	5	9
Low Temperature C- and N-lim Up	Aft2p	7.5E-04	10	34
Low Temperature C- and N-lim Up	Hsf1p	3.0E-08	16	133
Low Temperature C- and N-lim Up	Nrg1p	7.6E-07	14	128
Low Temperature C- and N-lim Up	Phd1p	3.3E-04	9	99
Low Temperature C- and N-lim Up	Rcs1p	1.1E-04	9	86
Low Temperature C- and N-lim Up	Rox1p	6.0E-05	8	62
Low Temperature C- and N-lim Up	Sok2p	5.7E-05	9	79
Low Temperature C- and N-lim Up	Nrg1-Aft2	6.0E-05	5	20
Low Temperature C- and N-lim Up	Phd1-Nrg1	1.4E-05	7	37
Low Temperature C- and N-lim Up	Rox1-Phd1	7.8E-05	5	21
Low Temperature C- and N-lim Up	Sok2-Nrg1	4.3E-07	8	33

(A) Significantly overrepresented cis-regulatory binding motifs in 5' upstream regions. (B) Significantly overrepresented promoter elements that bind known transcription factors (TF) or TF pairs according to ChIP-on-chip analysis (Harbison *et al.*, 2004). C-Lim, glucose-limited; N-Lim, ammonium-limited.

^a The number of occurrences of promoter element in the regulatory cluster.

^b Expected number of occurrences of the promoter element in a randomly chosen cluster of genes of the same cluster size.

^c The probability of finding the number of patterns with the same level of overrepresentation, which would be expected by chance alone.

^d Number of genes in category in cluster.

^e Number of genes in category in genome.

- **STRE elements exist in promoters of downregulated genes in N-limited cultures**
- **Upregulation in both conditions show PAC regulatory motifs in promoters**
- **Common promoter sequences show possible regulation relationships**

Genes Common to All Researchers Were Categorized According to Regulation

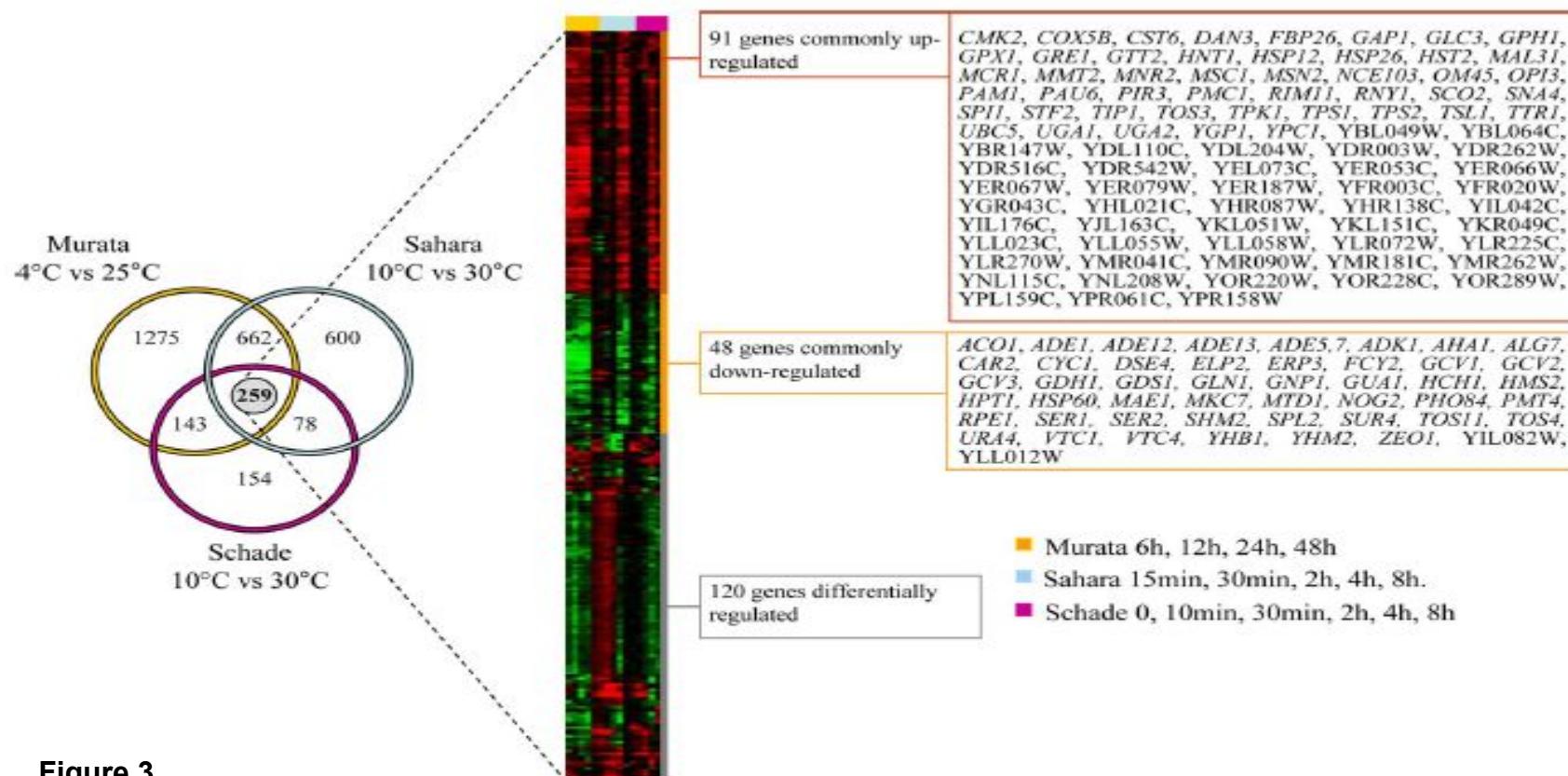


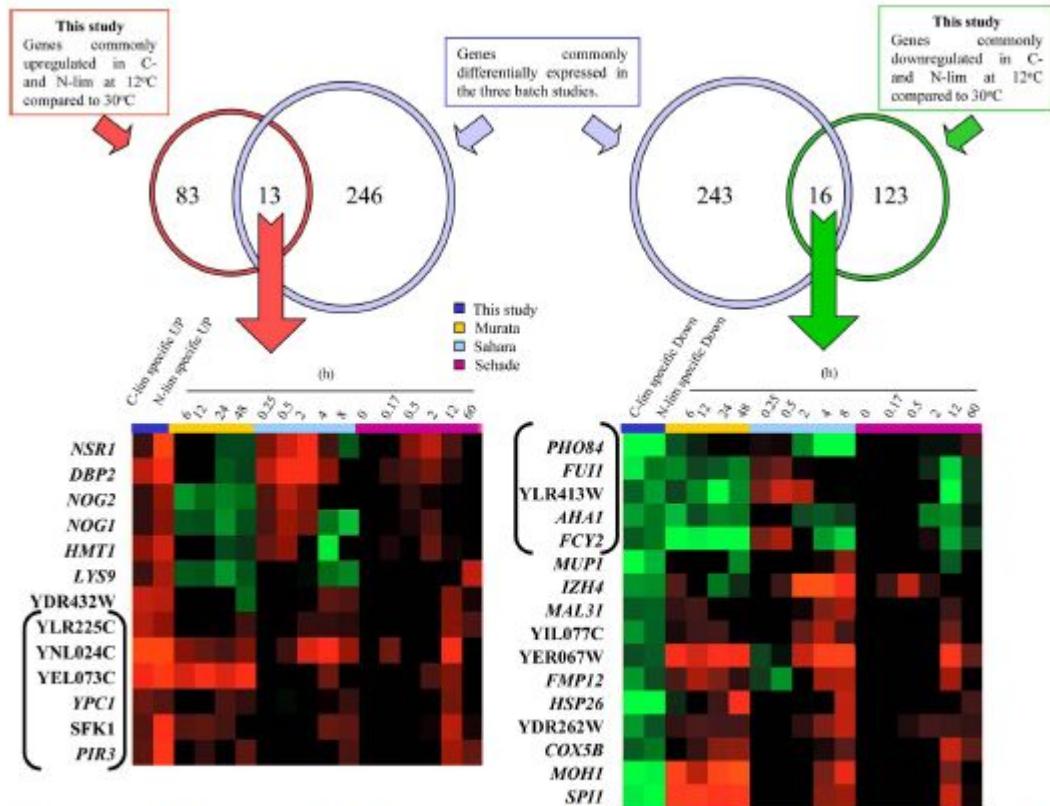
Figure 3

- Sahara and Schade tested cold shock, dropping temperature to between 10 and 20 degrees Celsius
- Murata tested cold shock at temperatures below 10 degrees Celsius, which caused cell growth to cease.

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Overlapping Genes Showing the Same Temperature Response



- **Chemostat study compared with Sahara et al. 2002, Schade et al. 2004, and Murata et al. 2006**
- **29 genes total were in common, only 11 showed consistency**

Figure 4

Few Genes Simultaneously Respond to Temperature and Growth Rate

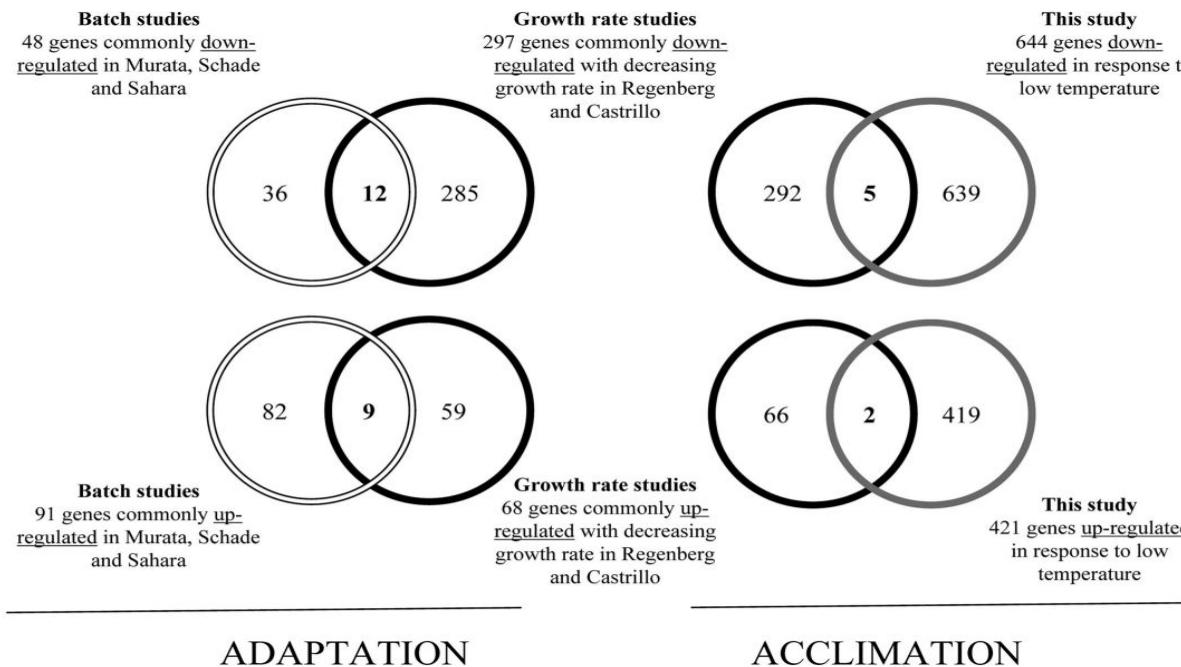


Figure 5

- Studies examined changes in gene regulation in response to a decrease in growth rate compared to both the batch studies and study data for overlap in gene regulation.
- A very small number of genes overlap in response to both temperature decrease and growth rate decrease.

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One Third of Low Temperature Response Genes in the Batch Studies are Attributed to ESR

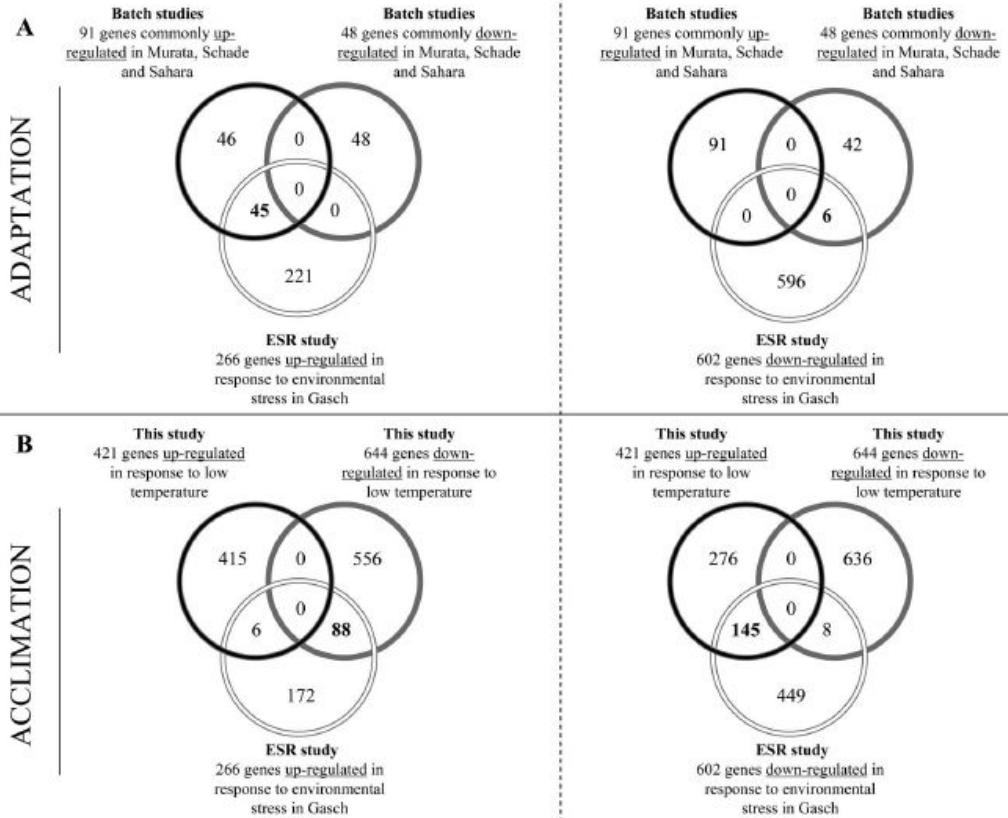


Figure 6

- **ESR: environmental stress response**
 - General mechanism responds to multiple stimuli
- **Batch and chemostat genes compared with Gasch et al. 2000**
- **Some genes showed opposite results in response to low temperatures**

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Experimental Design Differences Distinguish Dahlquist Lab Data from Tai et al. Data

	Dahlquist Lab	Tai et al.
Temperature	Cold Shock: 13°C Recovery: 30°C	Cold Shock: 12°C Recovery: 30°C
Time Points	15, 30, 60, 90, 120 min.	“Random Sampling”
Media	YPD rich media	Synthetic media limited by carbon or by nitrogen
Replicates	3-5 replicates	3 replicates
Strain	<i>S. cerevisiae</i> , Δgln3	<i>S. cerevisiae</i> strain CEN.PK113-7D

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25% of Δ gln3 Genes Showed Significant Difference In Expression Over Time

ANOVA	<i>d</i> GLN3
$p < 0.05$	2393 (38.7%)
$p < 0.01$	1453 (23.5%)
$p < 0.001$	696 (11.2%)
$p < 0.0001$	320 (5.2%)
B & H $p < 0.05$	1549 (25.0%)
Bonferroni $p < 0.05$	155 (2.5%)

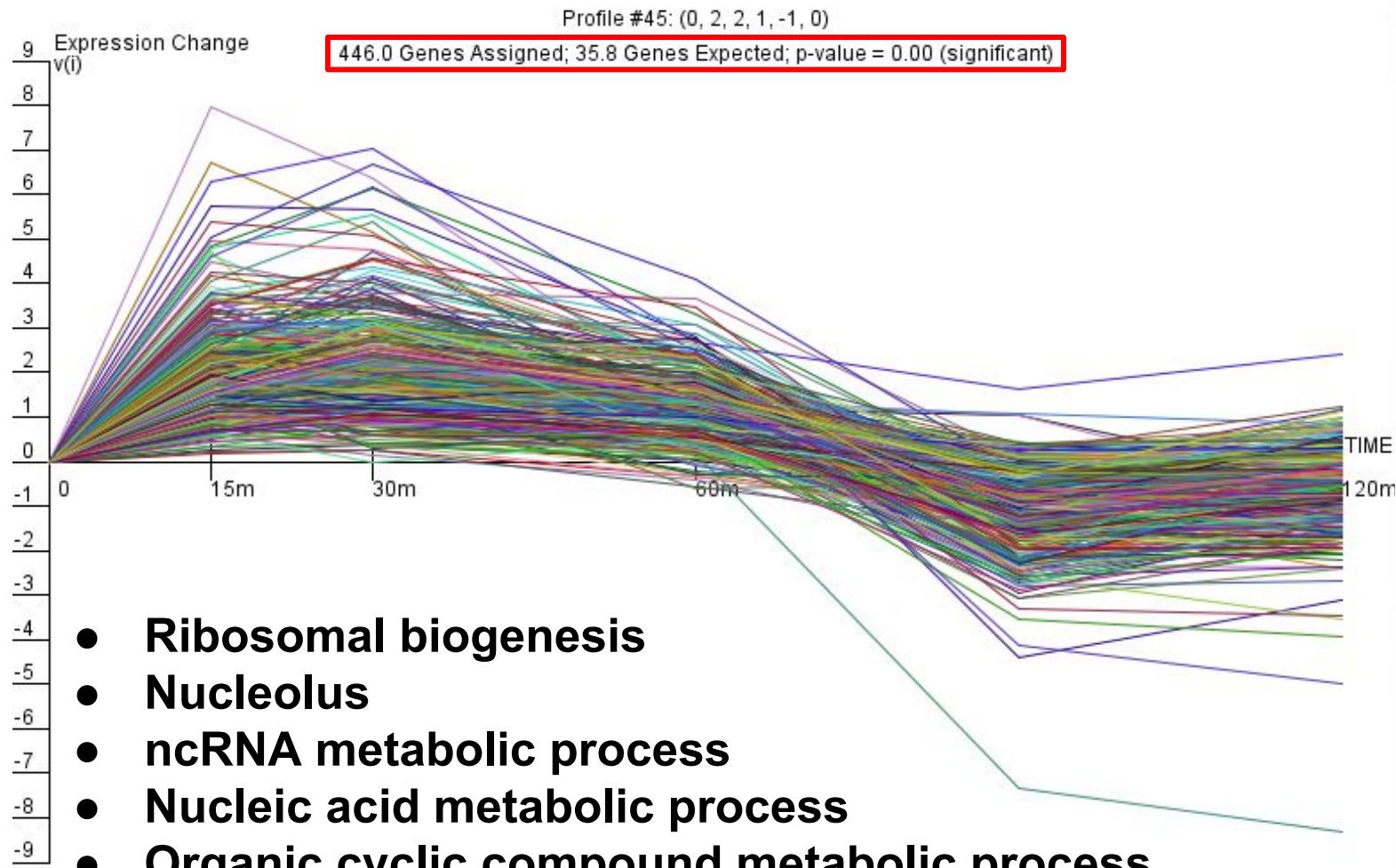
Genes Were Clustered According to Expression Pattern Using STEM Software



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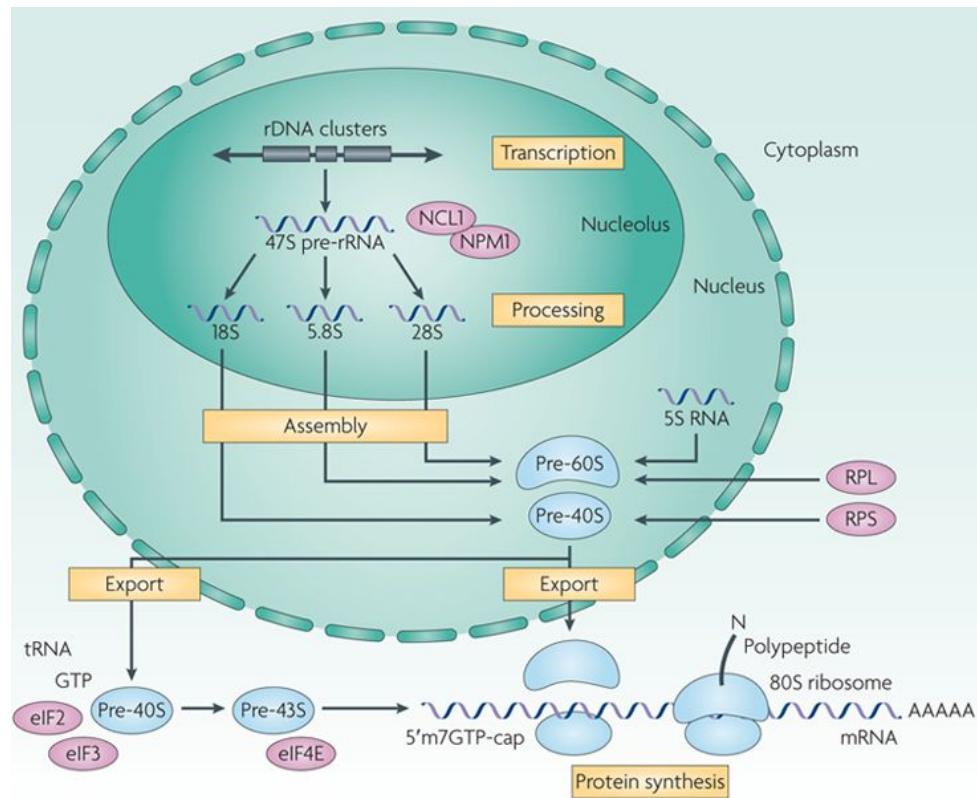
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Profile 45 Indicated Upregulation During Cold Shock and Down Regulation During Recovery



Ribosomal Biogenesis is Upregulated During Cold Shock in dGLN3

- Nucleolus: prime function is to transcribe nuclear DNA into 45S ribosomal precursor RNA and process RNA into 5.8S, 18S and 28S components
- ncRNA metabolic process: chemical reactions and pathways involving ncRNA transcripts
- Maturation of 5.8 rRNA from tricistronic rRNA transcript: processing of transcripts that contain small, large and 5.8S rRNA

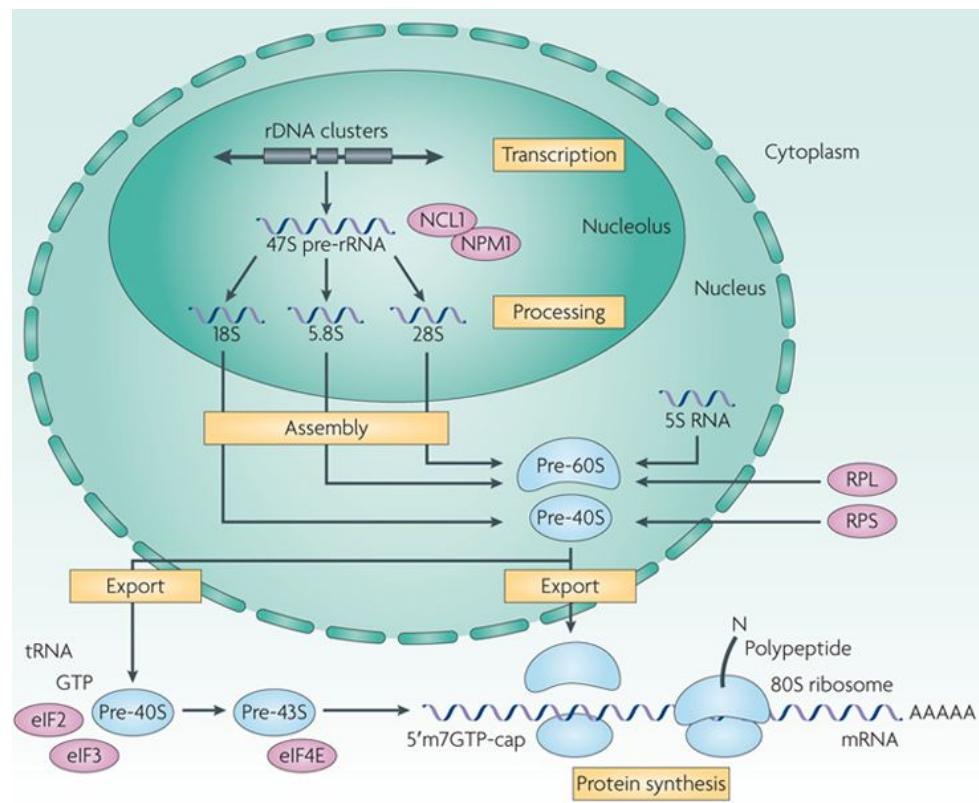


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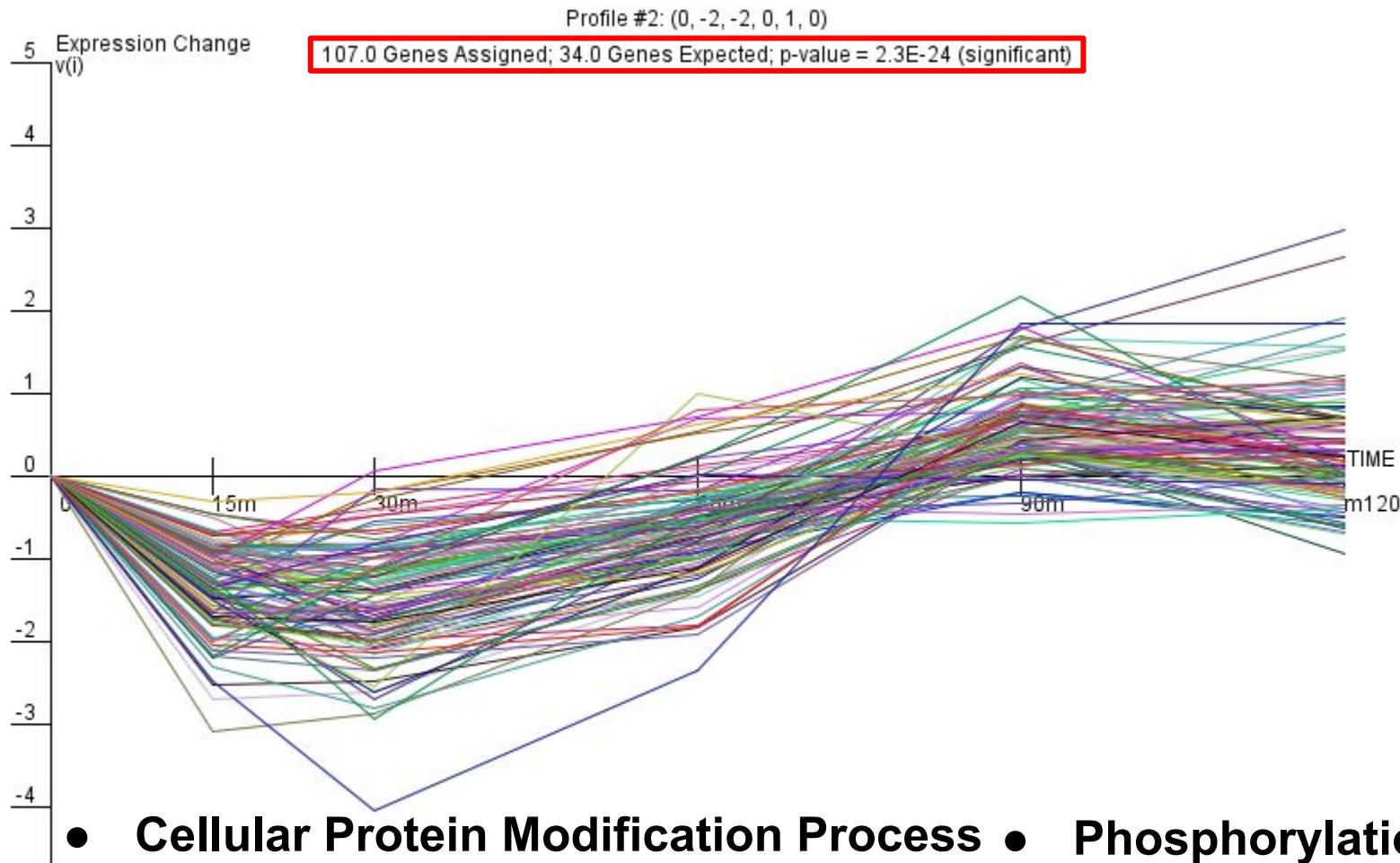
- Nucleic acid metabolic process
- Organic cyclic compound metabolic process
- Ribosomal biogenesis

- Increased ribosome genesis allows for increased protein expression
- Allows for cell to produce proteins that may protect it from cold shock
- Infanzon et al. (2010) found similar results



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Profile 2 Exhibits a Variance in DNA Replication During Onset of Cold Shock through Recovery

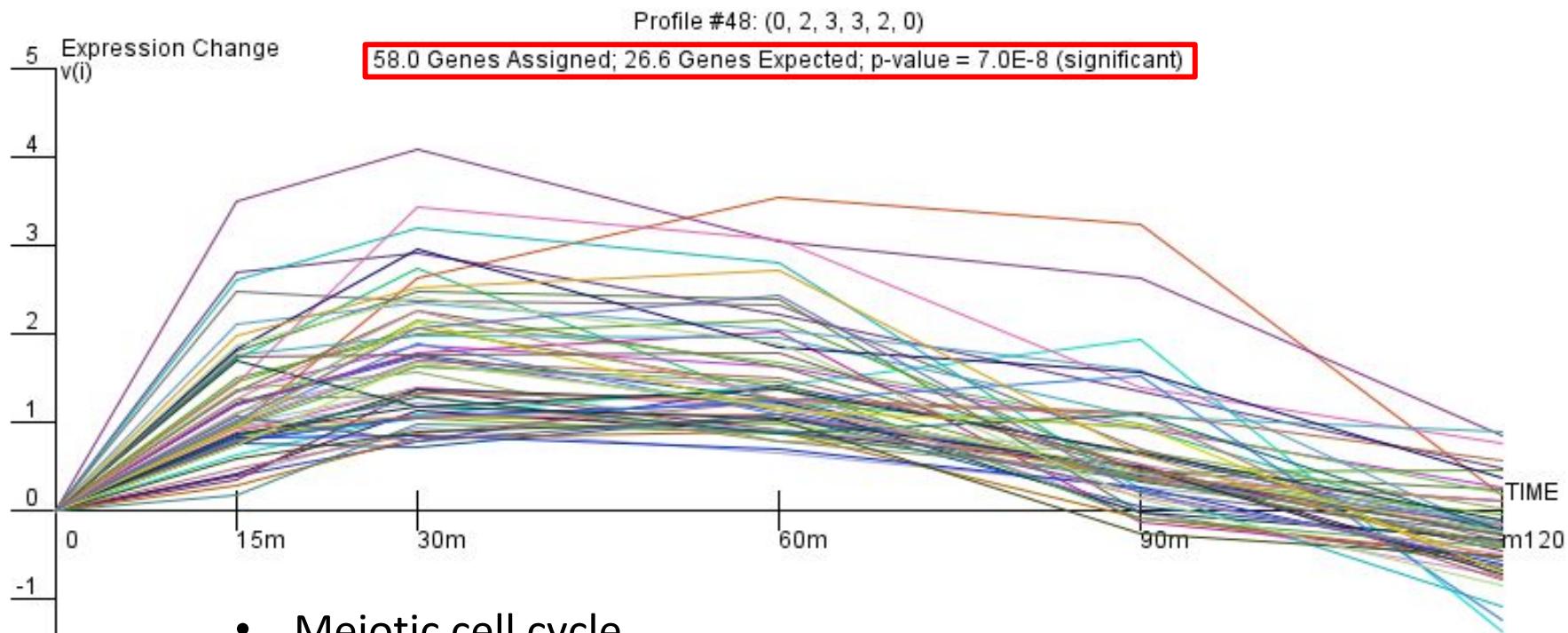


- Cellular Protein Modification Process
- Cytoplasmic Vesicle
- Mitotic Cell Cycle Phase Transition
- Phosphorylation
- DNA Replication
- Kinase Activity

DNA Synthesis is Initially Affected by Cold Shock then is Upregulated Through Recovery

- Down regulation followed by an upregulation
- DNA synthesis and related processes are repressed during the period of cold shock.
- The other processes seem to inform the overall theme of *DNA replication*.
 - This suggests that once the cells cleared the cold shock the cells were able to reactivate pathways of DNA synthesis in the cell cycle, indicating that the cells do not allocate resources for growth amidst the environmental stress.
 - During cold stress proteins bind to single-stranded regions of the replication fork and blocks DNA replication (Ermolenko 2002).

Profile 48 Shows Upregulation of Meiosis Related Processes

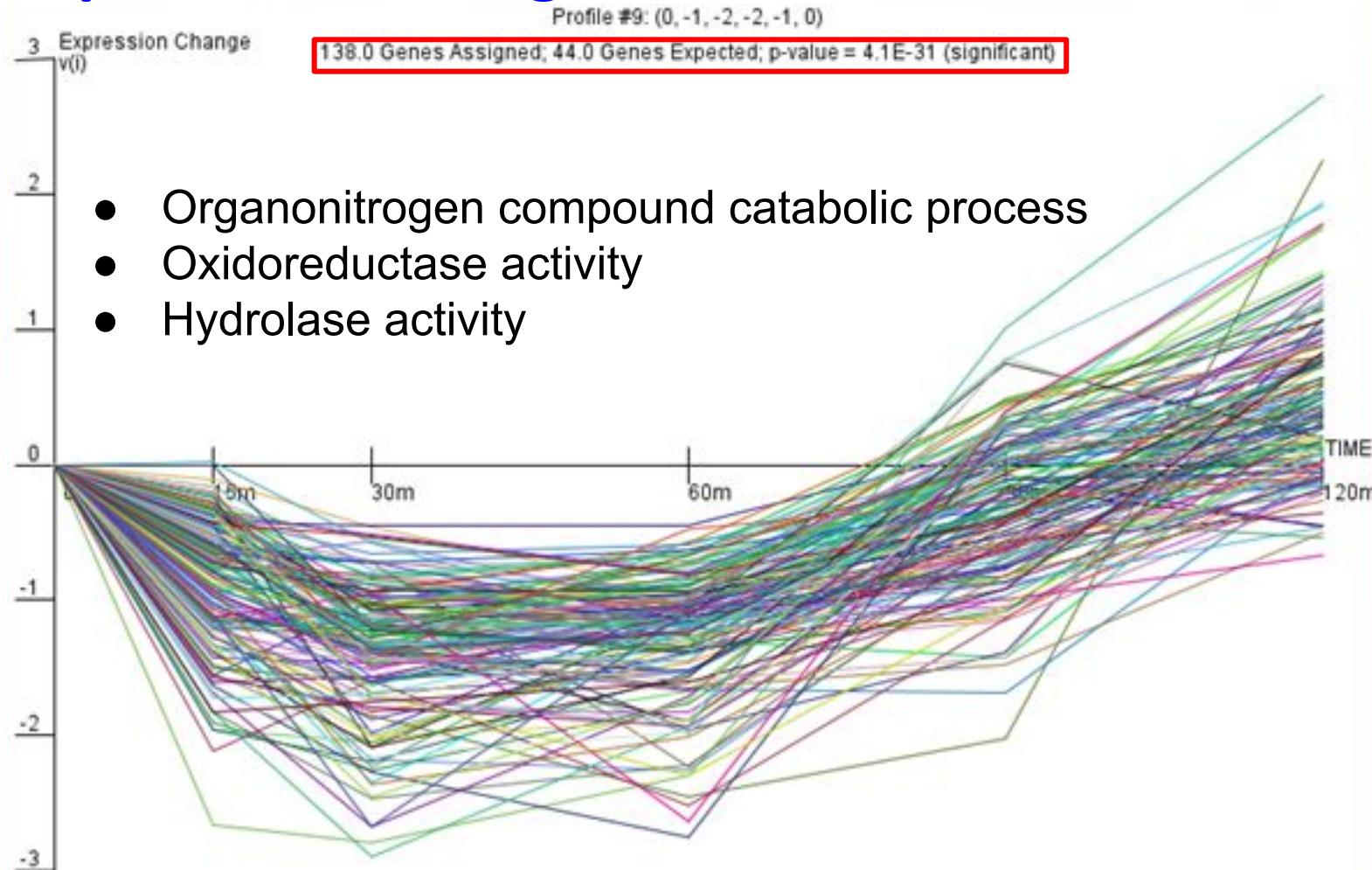


- Meiotic cell cycle
- Nuclear division
- Substrate-specific transmembrane transporter activity
- Intrinsic component of membrane
- DNA recombination
- Cellular component organization

Cold Stress Promoted Up-regulation of Meiosis Inhibiting Genes

- Overall Theme: Meiosis
- This profile's graph contains slight upregulation followed by a slight downregulation of genes associated with meiosis.
 - Down regulation occurs after cold shock.
- Cold stress may positively regulate meiosis, while it is known that heat stress will denature proteins and prevent meiosis.
 - Process has greater tolerance for colder temperatures.
- It is likely that cold stress causes inhibition of meiosis and related functions.
 - Research by Xiang-Ping Zhu et. al. suggests inhibition of meiosis during cold shock and then a return to normal functioning after temperature is readjusted.

Profile 9 Shows a Downregulation of Gene Expression During Cold Shock Time Points



- Organonitrogen compound catabolic process
- Oxidoreductase activity
- Hydrolase activity

- Carboxylic acid biosynthetic process
- Glutamine family amino acid metabolic process
- Transferase activity, transferring nitrogenous groups

Glutamine family amino acid biosynthesis was downregulated during cold shock

- Organonitrogen compound catabolic process: The chemical reactions and pathways resulting in the breakdown of organonitrogen compound
- Glutamine family amino acid biosynthesis: The chemical reactions and pathways resulting in the formation of amino acids of the glutamine family, comprising arginine, glutamate, glutamine and proline
- Glutamine based amino acids contain nitrogen
 - Decreased nitrogenous organic compound catalysis results in less nitrogen available for biosynthesis (Cai 2012)

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Ribosome Biogenesis, Mitosis, and Nitrogen Catabolism Genes Were Affected in Tai et al. and Dahlquist Lab

Tai et al.	Similarities	Dahlquist Lab
<p>Down regulation of target genes for glucose catabolite repression in cold shock conditions.</p>	<p>Genes involved with ribosome biogenesis and assembly upregulated in cold shock, but not in recovery.</p> <p>Down regulation of M-phase and chromosome segregation in cell cycle.</p> <p>Specific downregulation of genes responsible for nitrogen compound catabolism</p>	<p>Upregulation of genes related to meiosis inhibition.</p>

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Acknowledgments

Dr. Dahlquist
LMU Department of Biology
Sammi Flores



Good luck with finals!